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## A COMPARISON OF AUSTRALASIAN AND AMERICAN SPECIMENS OF *HEMISQUILLA ENSIGERA* (OWEN, 1832) (CRUSTACEA: STOMATOPODA)

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Drs. Raymond B. Manning, John C. Yaldwyn, and the present author each decided independently and simultaneously that the status of the Australian specimens of *Hemisquilla* merited reconsideration. Drs. Manning and Yaldwyn graciously consented to this author's undertaking the main investigation while at the Allan Hancock Foundation. Here, California material was available mostly from the Hancock Foundation collections. Australian material has been obtained from various museums in Australia (particularly the Australian Museum, Sydney). Chilean material was limited to the small, complete collection of the Smithsonian Institution; unfortunately no recent collections from Chile have been obtained. Dr. John C. Yaldwyn has kindly loaned me the only known New Zealand specimen.

Institutions referred to by abbreviations are: Allan Hancock Foundation (AHF); Australian Museum, Sydney (AM); Dominion Museum, Wellington (DM); Scripps Institution of Oceanography (SIO); United States National Museum, Smithsonian Institution (USNM).

Measurements throughout are in millimeters. Carapace lengths were measured with dial calipers, and other dimensions with the

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calibrated eyepiece of a stereomicroscope. Both are accurate to ca. 0.1 mm.

Two considerations are involved: first, whether the material from Australia and New Zealand (i.e. Australasia) is identical with the American, and secondly, what names to apply to the different populations.

The author is deeply grateful to Drs. Raymond B. Manning and John C. Yaldwyn for helpful suggestions, to Miss May Rees for assistance in computations, and to Mr. I. F. Horton for advice on statistical matters. Thanks are also due to the directors and curators of Crustacea of the above-mentioned institutions for allowing me to examine their *Hemisquilla* collections. I also wish to thank the directors and curators of Crustacea of institutions not mentioned: Johns Hopkins Marine Laboratory, the Queensland Museum, Brisbane, and the Tasmanian Museum, Hobart.

#### Names of Chilean Material

At the generic level the following names have been employed: *Gonodactylus* Latreille, 1825 (e.g., by H. M. Edwards, 1837; Nicolet, 1849; Miers, 1880; and Bigelow, 1894); *Pseudosquilla* Dana, 1852 (e.g., by Rathbun, 1910; Kemp, 1913) and *Hemisquilla* Hansen, 1895 (e.g., by Schmitt, 1940; and Manning, 1963b).

Most workers have used the specific epithets *styliferus* or *stylifera*, following H. M. Edwards' (1837) description of *Gonodactylus styliferus*. Rathbun (1910) showed that *G. styliferus* H. M. Edwards is a homonym of *G. styliferus* (Lamarck, 1818), now *Pseudosquilla ciliata* (Fabricius, 1787). She substituted the specific epithet *bigelowi*, and *Gonodactylus styliferus* H. M. Edwards became *Pseudosquilla bigelowi* Rathbun. This name has been used by a number of American workers for Californian material (e.g., Hilton, 1915a, 1915b; Buchsbaum and Milne, 1960).

Meanwhile Australian records have been under *P. stylifera* (H. M. Edwards) by Whitelegge (1900) and Kemp (1913); and under *H. stylifera* (H. M. Edwards) (following Schmitt, 1940) by Stephenson (1953, 1954) and Stephenson and McNeill (1955).

Manning (1963b) has shown that *Gonodactylus ensiger* Owen, 1832, from Chile is clearly the *Hemisquilla* that H. M. Edwards described as *G. styliferus*. Manning stressed the color similarities between Owen's description and preserved Chilean material, which leaves no doubt that *Hemisquilla ensigera* (Owen, 1832) has priority as the name for the Chilean form. He is also using this name for Australian material (Manning, 1967).

### Distribution

Randall's (1839) Hawaiian record, suggesting continuous pan-Pacific distribution has been shown by Manning (1963b) to have been based upon an incorrectly labelled American specimen. Evidently Australasian and American populations are geographically distinct.

Past American records show a discontinuous antitropical distribution, with distinct Californian and Chilean records, the latter including Juan Fernandez (see Schmitt, 1940). One specimen, collected by the Allan Hancock Foundation, links these populations by the following measurements: juvenile, anterior half of body only, carapace length 6.0 mm, rostral length 1.7 mm, rostral breadth 1.7 mm, length eye 3.0 mm, length eyestalk 2.3 mm, length cornea 2.5 mm, breadth cornea 2.3 mm, no mandibular palps visible. Other data are: Jicarita Is., Panama, dredging east side, 24 fms, shelly gravel, coll. W. L. Schmitt, Hancock Galapagos Exped., *Velero* Sta. 240-34, Feb. 20, 1934, USNM 76381. This specimen is obviously a *Hemisquilla* as evidenced by (1) the raptorial claw having a single terminal tooth and not being swollen basally, (2) the articulation between the merus and ischium being terminal, (3) the carapace lacking carinae, and (4) the detailed structure of the narrowest part of the cornea (see p. 10) being identical with that of specimens of *H. ensigera*. Apart from the unlikely event of the first specimen of an undescribed species being a damaged juvenile, it must belong to *H. ensigera*.

Although only 37 specimens have been available for study, it is evident that the species is common in the Californian region. The California Department of Fisheries and Game advise that it is frequently caught on rod and line (one was so caught in the author's presence) and by skin divers. Verbal confirmation has been received from various unofficial sources. The contrast between apparent abundance and numbers available for study from this region suggests the possibility that additional specimens may be recovered from Central American waters in future years. Present records certainly extend the known southern limit of the Californian population, as evidenced by the following specimens all recently obtained from Mexican waters:

(1) ♂, east side of North Coronados Is., lower Calif., fishing line at 100 ft (33 m), Aug. 20, 1949, coll. John L. Perkins, RI 6.2-6 (SIO).

(2) ♂, Ensenada, lower Calif., Feb. 10, 1958, RI 6.2-11 (SIO).

(3) 2 ♂♂, 5.4 mi E Morro Redondo Pt., Cedros Is., 41 fms (74 m), trawl, Apr. 20, 1951, *Velero* Sta. 2030-51 (AHF).

(4) ♂, Sebastian Vizcaino Bay, lower Calif., coll. Jack Littlepage, acc. no. 153 (AHF).

(5) 2 ♂♂, 3 ♀♀, San Cristobal Bay, lower Calif., 41 fms (74 m), trawl, Apr. 27, 1950, *Velero* Sta. 1949-50 (AHF).

(6) ♂, ♀, 1 juvenile, 27°24' N, 114°40' W, San Cristobal Bay, lower Calif., 40 fms (72 m), Aug. 20, 1960 (1800-1820 hrs.), otter trawl, 6008B, 123.37, coll. Fred Berry (SIO).

(7) ♂, Turtle Bay, lower Calif., in purse seine inside bay during daytime, *Stella Maris*, coll. Ben Fukuzaki (AHF).

(8) ♀, 6.25 mi SSW San Hipolito Pt., 36 fms (65 m), trawl, Apr. 29, 1950, *Velero* Sta. 1952-50 (AHF).

The following specimen, kindly loaned by Dr. John C. Yaldwyn, is the first recorded from New Zealand: ♀, New Zealand waters, DM reg. no. Z.Cr.1493.

### Morphological Differences—Initial Study

Only four possible distinguishing features were noted on preserved specimens from different areas. In each case there was considerable variability and such overlap between the series that statistical analyses were deemed necessary.

Initially, comparisons were made between Australasian and American material. Chilean and Californian collections were pooled for the following reasons: (1) the single Panamanian specimen tends to bridge the biogeographic gap; (2) probably the northern population extends in strength beyond the known southern limit as evidenced by the fact that 15 of the 37 "Californian" specimens have been collected in recent years in Mexican waters; and (3) the small number of Chilean specimens (9 only) available for study.

In each case a quantitative study of a feature was made and group means were computed. In most cases deviations from means exhibited by each of the individuals in a group were plotted as frequency distribution histograms; in other cases raw data were plotted similarly. These histograms sometimes indicate differences in the constitution of populations from the two areas (figs. 1-3). Histograms showing normal distributions are not given.

Variabilities of populations were computed in terms of standard deviations divided by means; these again indicate some population differences.

Finally, *t* tests of the significance of differences between group means were carried out (Lacey, 1953, p. 114; Fisher and Yates, 1957). It is appreciated that the applicability of this test is affected by abnormal frequency distributions; however, the low *p* values obtained

in all relevant cases ( $p \ll 0.001$ ) leave no doubt of the significance of the differences.

In certain cases inspection of raw data indicated the possibility of sexual dimorphism. Means for Australasian males and females and for American males and females, respectively, were computed and  $t$  tests carried out in "promising" cases within the locality groupings.

In other cases it was suspected that the measured ratios depended upon specimen size. Using all specimens from a given area, correlation coefficients were computed between ratios and carapace length (i.e., the measure of specimen size) and were tested for significance (Fisher and Yates, 1957). Regression coefficients were computed in several cases.

**MANDIBULAR PALP.**—Kemp (1913) noted two-segmented palps in an Australian specimen and from one to three segments in Chilean specimens. Schmitt (1940) noted three segments on the right and two on the left side of a single Southern Californian specimen.

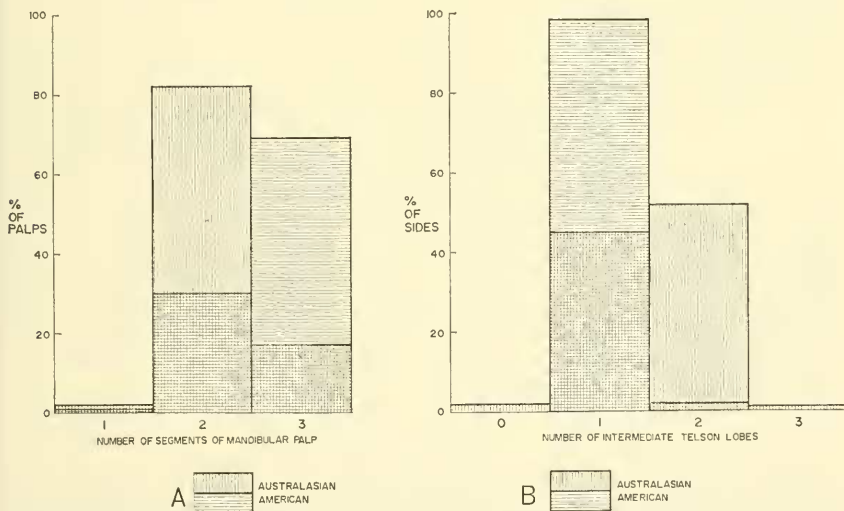


FIGURE 1.—Frequency distribution histogram showing percentages of specimens with varying numbers of: A, segments of mandibular palp; B, intermediate telson lobes.

Figure 1A shows that the Australasian population gives an approximately normal distribution curve with a mode of about two segments, but the American is strongly skewed to the right. Table 1 indicates approximately equal variability in the two populations. On the difference between means,  $t$  tests give  $p \ll 0.001$ . There is no doubt that the specimens belong to populations that are statistically separate.



Inspection of raw data gave no indications of differences between sizes or sexes of specimens, and analyses were not attempted. A minor cause of variation is related to loss and regrowth of palps. While many of the palps missing from the specimens may have been removed during collection and preservation, the occasional presence of unusually small palps, typically weakly segmented, suggests that natural loss and regrowth can occur. This could reflect varying environmental stresses, apart from any genetical differences.

TABLE 1.—*Comparative data of Australasian and American specimens*

|                                             | No. of segments of mandibular palp |        | Intermediate telson lobes |        | L/B rostrum |           |
|---------------------------------------------|------------------------------------|--------|---------------------------|--------|-------------|-----------|
|                                             | Aust.                              | Amer.  | Aust.                     | Amer.  | Aust.       | Amer.     |
| Mean                                        | 2.3558                             | 2.6777 | 1.3559                    | 1.0220 | 1.1021      | 1.3037    |
| <i>n</i>                                    | 104                                | 90     | 118                       | 91     | 59          | 44        |
| Range                                       | 1-3                                | 1-3    | 0-3                       | 1-2    | 0.88-1.26   | 1.10-1.54 |
| Standard deviation                          | 0.473                              | 0.491  | 0.612                     | 0.147  | 0.0821      | 0.134     |
| <u>Standard deviation</u><br>mean           | 0.201                              | 0.183  | 0.451                     | 0.143  | 0.0745      | 0.103     |
| Probability of differences ( <i>t</i> test) | <<0.001                            |        | <<0.001                   |        | <<0.001     |           |

|                                             | <u>L carapace</u><br>L rostrum |          | L/B cornea |           | <u>L eye</u><br>B cornea |           |
|---------------------------------------------|--------------------------------|----------|------------|-----------|--------------------------|-----------|
|                                             | Aust.                          | Amer.    | Aust.      | Amer.     | Aust.                    | Amer.     |
| Mean                                        | 4.7746                         | 4.1534   | 1.2013     | 1.3090    | 1.3230                   | 1.4679    |
| <i>n</i>                                    | 59                             | 44       | 55         | 41        | 54                       | 42        |
| Range                                       | 4.0-6.0                        | 3.50-5.0 | 1.08-1.36  | 1.04-1.55 | 1.08-1.46                | 1.12-1.92 |
| Standard deviation                          | 0.442                          | 0.371    | 0.0589     | 0.340     | 0.0733                   | 0.283     |
| <u>Standard deviation</u><br>mean           | 0.0926                         | 0.0893   | 0.0490     | 0.260     | 0.0554                   | 0.193     |
| Probability of differences ( <i>t</i> test) | <<0.001                        |          | <<0.001    |           | <<0.001                  |           |

INTERMEDIATE LOBES OF TELSON.—Kemp (1913) noted that an Australian specimen had two lobes on each side but the then known Chilean specimens had single lobes. Schmitt (1940, p. 181) noted single lobes on Southern California specimens and suggested that these differences might be "of more significance than may seem justified at present."

In counting numbers of lobes, difficulties were encountered over two American and one Australian specimen. These possessed on each side one normal lobe and one very small lobe just lateral to it; the latter were regarded as vestigial and were not counted. In addition, one side of an American specimen had a malformed telson, and this was excluded from the count.

Figure 1B shows that the Australasian population gives a skewed curve but the American an approximately normal curve. (This is the opposite of results shown in figure 1A). Table 1 shows that the Australasian data vary more than the American. Differences between means are again significant with  $p \ll 0.001$ , and the populations are again statistically distinct.

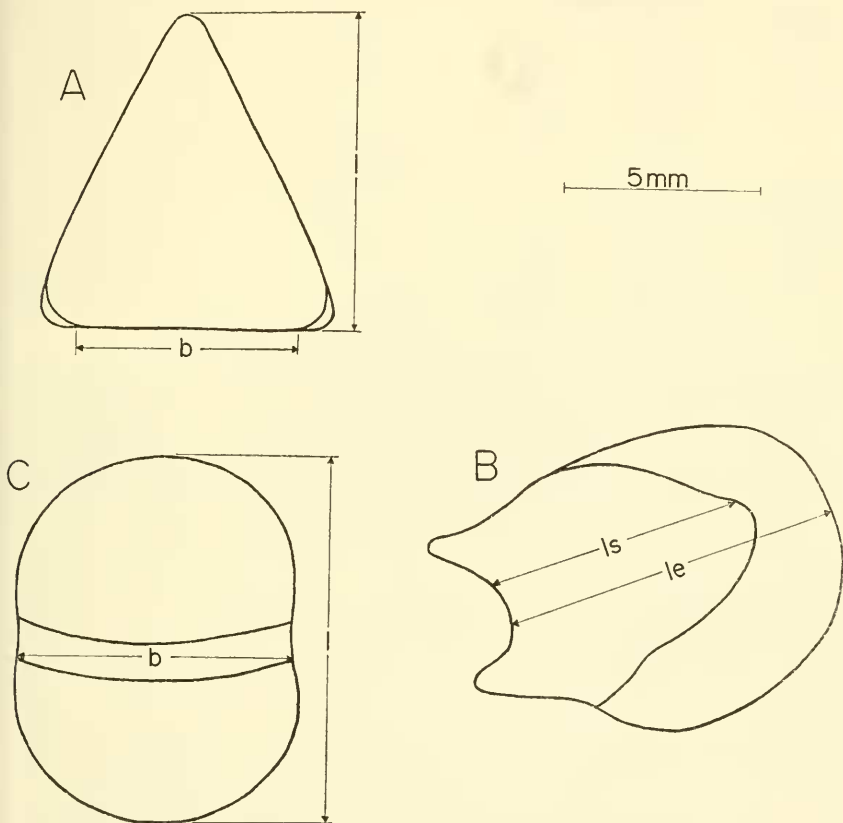


FIGURE 2.—Dimensions of *Hemisquilla ensigera*: A, rostrum; B, eye, lateral view; C, cornea, anteroventral view (l=length, b=breadth, le=length of eye, ls=length of eyestalk; drawn from male, Queensland Mus. reg. no. W1779).

**ROSTRAL PROPORTIONS.**—This distinction was suggested initially by comparison of Australian specimens with Kemp's figure (1913, pl. 7, fig. 84) of a Chilean specimen.

All specimens were measured for lengths and breadths of rostrum and carapace lengths. Measuring rostral breadths caused occasional difficulty and basal breadths on the upper surface of the line of articulation with the carapace were measured in preference to maxi-

mum breadth (fig. 2A). From these measurements, the ratios  $L/B$  rostrum and  $L$  carapace/ $L$  rostrum were computed.

Selected data show a hint of bimodality in the Australasian data (fig. 3A) and a much less definite hint in the American (fig. 3B). The

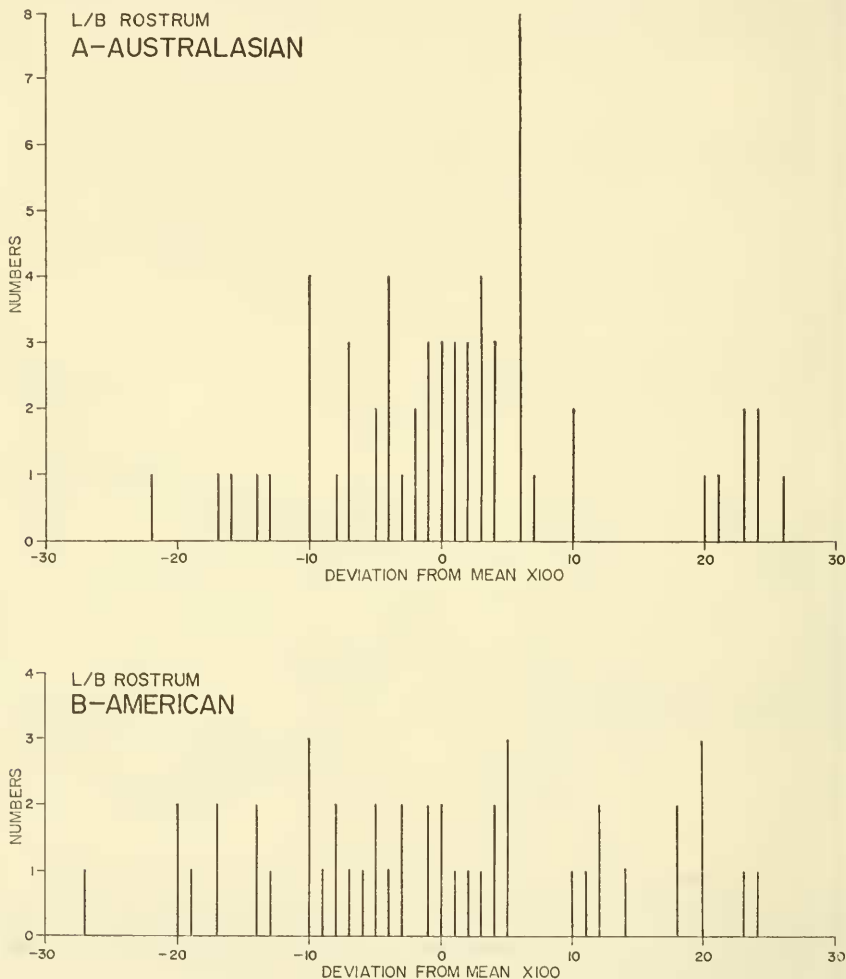


FIGURE 3.—Frequency distribution histograms showing numbers of Australasian and American specimens with varying deviations from group mean  $L/B$  ratios.

small "separate" groups with higher deviations are not distinctive as regards sex ratio or size; to simplify analyses, hints of polymorphism in  $L/B$  rostrum data were ignored. There are no comparable hints in  $L$  carapace/ $L$  rostrum data.



Table 1 shows that there is equivalent variability in Australasian and American material and that the rostra of American specimens are significantly longer than that of the Australasian ( $p. \ll 0.001$ ).

Inspection of data indicated possible sexual dimorphism and size effects. Relevant data on sexual differences are shown below.

| L/B rostrum |        |        |               |
|-------------|--------|--------|---------------|
|             | no.    | mean   | weighted mean |
| Australasia | 36 ♂ ♂ | 1.1017 | 1.1021        |
|             | 23 ♀ ♀ | 1.1026 |               |
| America     | 28 ♂ ♂ | 1.3086 | 1.3027        |
|             | 16 ♀ ♀ | 1.2925 |               |

| L carapace/L rostrum |        |        |               |
|----------------------|--------|--------|---------------|
|                      | no.    | mean   | weighted mean |
| Australasia          | 36 ♂ ♂ | 4.7292 | 4.7746        |
|                      | 23 ♀ ♀ | 4.8457 |               |
| America              | 28 ♂ ♂ | 4.1289 | 4.1534        |
|                      | 16 ♀ ♀ | 4.1963 |               |

For L carapace/L rostrum data the differences between male and female means is significant almost at the 0.02 level on Australasian material but not significant on American ( $p$  ca. 0.3). No tests were carried out on L/B rostrum data because of the small differences between means of Australasian males and females, respectively, and the reversed tendency of Australasian versus Californian data.

The effects of size upon the ratios were only investigated upon L/B rostrum data, which appeared to offer the more "promising" indications. Correlation coefficients between carapace length and L/B rostrum for Australasian and American material are  $-0.070$  and  $+0.330$ , respectively. The former is not significant ( $p > 0.1$ ), while the latter is significant at about the 0.03 level. Regression coefficients between carapace length and L/B rostrum are  $-0.00156$  and  $+0.00479$ , respectively.

Summarizing these analyses, the American and Australasian specimens clearly belong to different populations with shorter rostra on the Australasian material. There are indications of sexual dimorphism, with a smaller L carapace/L rostrum ratio in males, but this is significant only on Australasian material. There are also indications of a slight size effect, which is significant only on American material.

EYES AND EYESTALKS.—This possible distinction, like the last, arose initially by comparison of Australasian specimens with Kemp's figure (1913, pl. 7, fig. 84) of a Chilean specimen.

Measurements were made on all undamaged eyes of length of eyestalk from lateral view, length of entire eye from lateral view,

length of cornea from anteroventral view (looking at cornea "end on"), and breadth of cornea in similar view (see figs. 3B, C). Choice of the portions of the eye to be measured was conditioned partly by ease of precise recognition on successive occasions. Thus minimal corneal breadth was measured because recognition is aided by slight concave curvatures in the centers of the corneas, by the presence of larger facets in this area, and by transverse pigment lines in pigmented specimens. In all measurements there are subjective errors, and the accuracy of results decreases, possibly to  $\pm 0.2$  mm. From these measurements L/B cornea and L eye/B cornea were computed as the most accurate and meaningful of the possible ratios.

Histograms of deviations from means give normal frequency distributions in each case. Values of standard deviation/mean (table 1) indicate that for L/B cornea data only the American material varies more than the Australasian. For both L/B cornea and L eye/B cornea data American specimens give higher values than Australasian, with the differences significant at values of  $p \ll 0.001$ .

Inspection of data indicated possible sexual dimorphism and possible size effects. Relevant data on sexual differences are shown below.

#### L/B cornea

|             | no.    | mean   | weighted mean |
|-------------|--------|--------|---------------|
| Australasia | 32 ♂ ♂ | 1.2028 | 1.2013        |
|             | 23 ♀ ♀ | 1.1991 |               |
| American    | 25 ♂ ♂ | 1.3092 | 1.3090        |
|             | 16 ♀ ♀ | 1.3088 |               |

#### L eye/B cornea

|             | no.    | mean   | weighted mean |
|-------------|--------|--------|---------------|
| Australasia | 31 ♂ ♂ | 1.3277 | 1.3230        |
|             | 23 ♀ ♀ | 1.3143 |               |
| American    | 25 ♂ ♂ | 1.4772 | 1.4679        |
|             | 17 ♀ ♀ | 1.4512 |               |

For L/B cornea data, differences between the means of males and females are not significant either upon Australian material ( $p$  ca. 0.6) or American ( $p \gg 0.9$  level). For L eye/B cornea Australian data significance is at the 0.1 level but American data are not significantly different ( $p \gg 0.9$ ).

Size effects were investigated only on L/B cornea data. The correlation coefficient between carapace length and L/B cornea for Australasian specimens is 0.296 ( $p$  ca. 0.02) and for American 0.476 ( $p \ll 0.001$ ). Regression coefficients are 0.00145 and 0.00562, respectively.

Summarizing these analyses, the American and Australasian specimens clearly belong to different populations as indicated by the

dimensions of eyes and eyestalks (broader cornea in Australasian material). Of four possibilities of sexual dimorphism, only one is significant—L eye/B cornea in Australasian males, greater than in females. The ratio L/B cornea increases significantly with specimen size.

The general summation of the results of the present section is that Australasian and American material are significantly different in all features selected for examination. In the six sets of data, differences between means are significant at  $p$  levels of  $\leq 0.001$ . Apart from differences in means there are also differences in the form of frequency distributions of deviations from mean (e.g., skewness) and in heterogeneity within groups. There are indications of sexual dimorphism in certain features and stronger indications of proportions changing with specimen size. Since none of these effects are as noteworthy as those depending upon locality, they were neglected in further analyses.

### Comparisons Between Californian, Chilean, and Australasian Material

Because differences between American and Australasian populations had proved so highly significant and because in many respects mean values for Chilean material lay between Californian and Australasian extremes, data were reconsidered under the three main locality groupings. Results, given in tables 2 and 3, show that differences between Californian and Australasian data are highly significant throughout. Further consideration is restricted to Australasian/Chilean and Chilean/Californian comparisons.

MANDIBULAR PALP.—The mean Chilean value is roughly midway between Australasian and Californian means, with an approximately equal probability of the differences being significant ( $p$  ca. 0.1 and 0.2 – 0.1, respectively). The three populations have approximately equivalent variability. The Californian data is more skewed than the Chilean data.

INTERMEDIATE LOBES OF TELSON.—The mean Chilean value lies further from the Australasian than the Californian and differs significantly from the Australasian ( $p$  ca. 0.01) but not from the Californian ( $p$  0.4 – 0.3). The Chilean data resembles the Californian in the form of its frequency distribution; both differ from the skewed curve for Australasian data. Variability in the Australasian data is much higher than in the Chilean, which resembles more that of the Californian.

ROSTRAL PROPORTIONS.—L/B rostrum: The mean Chilean value is closer to the Australasian than to the Californian. It is not significantly different from the former ( $p$  ca. 0.2) but is from the latter ( $p \leq 0.001$ ). The variability of the Chilean values is of the same

order of magnitude as for the Australasian and is considerably smaller than the Californian.

L carapace/L rostrum: Again the mean Chilean value is closer to the Australasian than to the Californian. It is just significantly different from the former ( $p$  ca. 0.1) but is highly significantly different from the latter ( $p \ll 0.001$ ). Variability is approximately the same throughout.

EYES AND EYESTALKS.—L/B cornea: The mean Chilean value is midway between Australasian and Californian values, with differences significant in both cases ( $p$  ca. 0.001 and  $< 0.05$ , respectively). Varia-

TABLE 2.—Comparative data of Australasian, Chilean, and Californian specimens

|                            | No. of segments of mandibular palp |        |        | Intermediate telson lobes |       |        | L/B rostrum   |               |               |
|----------------------------|------------------------------------|--------|--------|---------------------------|-------|--------|---------------|---------------|---------------|
|                            | Aust.                              | Chile  | Calif. | Aust.                     | Chile | Calif. | Aust.         | Chile         | Calif.        |
| Mean                       | 2.3558                             | 2.5500 | 2.7083 | 1.3559                    | 1.0   | 1.0274 | 1.1021        | 1.1744        | 1.3357        |
| <i>n</i>                   | 104                                | 18     | 72     | 118                       | 18    | 73     | 59            | 9             | 35            |
| Range                      | 1-3                                | 2-3    | 1-3    | 0-3                       | 1     | 1-2    | 0.88-<br>1.26 | 1.10-<br>1.29 | 1.10-<br>1.54 |
| Standard deviation         | 0.473                              | 0.497  | 0.484  | 0.612                     | 0     | 0.163  | 0.0821        | 0.0678        | 0.112         |
| Standard deviation<br>mean | 0.201                              | 0.194  | 0.179  | 0.451                     | 0     | 0.159  | 0.0745        | 0.0577        | 0.0839        |

|                            | L carapace<br>L rostrum |              |               | L/B cornea    |               |               | L eye<br>B cornea |               |               |
|----------------------------|-------------------------|--------------|---------------|---------------|---------------|---------------|-------------------|---------------|---------------|
|                            | Aust.                   | Chile        | Calif.        | Aust.         | Chile         | Calif.        | Aust.             | Chile         | Calif.        |
| Mean                       | 4.7746                  | 4.5388       | 4.0543        | 1.2013        | 1.2689        | 1.3203        | 1.3220            | 1.5056        | 1.4576        |
| <i>n</i>                   | 59                      | 9            | 35            | 55            | 9             | 32            | 54                | 9             | 33            |
| Range                      | 4.0-<br>6.0             | 4.1-<br>5.15 | 3.50-<br>4.57 | 1.08-<br>1.36 | 1.18-<br>1.38 | 0.95-<br>1.55 | 1.08-<br>1.46     | 1.41-<br>1.65 | 1.12-<br>1.92 |
| Standard deviation         | 0.442                   | 0.3376       | 0.3046        | 0.0589        | 0.0617        | 0.0931        | 0.0733            | 0.0782        | 0.3123        |
| Standard deviation<br>mean | 0.0926                  | 0.0744       | 0.0750        | 0.0490        | 0.0486        | 0.0705        | 0.0554            | 0.0519        | 0.2140        |

bilities of Australasian and Chilean material are roughly the same and lower than Californian.

L eye/B cornea: The Chilean mean is further from the Australasian than is the Californian;  $p$  values emphasize the difference between Chilean and Australasian material ( $p \ll 0.001$ ) and the similarity between Chilean and Californian ( $p$  0.6 - 0.5). The variability of the Californian population is much greater than that of either of the others.

Summarizing these results, of the six determinations upon the four selected structural features, in four the mean Chilean values lie between the extremes of the Australasian and the Californian, and in the other two they lie further from the Australasian than do the

Californian. In significance tests in 5/6 cases, differences between Chilean and Australasian means are significant, and in one case (L/B rostrum) they just fail to be significant ( $p$  ca. 0.2). In 2/6 cases differences between Chilean and Californian means are not significant, in one case the difference just fails to be significant, and in two cases differences are highly significant.

### Comparisons Between *H. ensigera* and *H. braziliensis*

In deciding the status to be given to the three populations of *H. ensigera*, two considerations are relevant:

(1) Distinctions between stomatopod taxa are becoming finer from the generic level downward (Serène, 1962; Manning, 1963a).

(2) *H. ensigera* is very close to *H. braziliensis* (Moreira, 1903a, b), the only other species of the genus. The only conspicuous difference in preserved material is that in *H. braziliensis* the lobes of the telson

TABLE 3.—Significance of differences among three populations of *H. ensigera*

|                |          | No. of<br>segments<br>of man-<br>dibular<br>palp | Inter-<br>mediate<br>telson lobes | L/B<br>rostrum | L carapace<br>L rostrum | L/B<br>cornea | L eye<br>B cornea |
|----------------|----------|--------------------------------------------------|-----------------------------------|----------------|-------------------------|---------------|-------------------|
| Australasia    | <i>t</i> | 1.784                                            | 2.870                             | 1.377          | 1.651                   | 3.674         | 8.088             |
| v. Chile       | <i>p</i> | c. 0.1                                           | c. 0.01                           | c. 0.2         | c. 0.1                  | c. 0.001      | <<0.001           |
| Chile v.       | <i>t</i> | 1.527                                            | 0.932                             | 5.220          | 5.295                   | 2.032         | 0.591             |
| Californian    | <i>p</i> | 0.2-0.1                                          | 0.4-0.3                           | <<0.001        | <<0.001                 | <0.05         | 0.6-0.5           |
| Californian    | <i>t</i> | 11.226                                           | 9.176                             | 22.680         | 15.727                  | 13.538        | 6.164             |
| v. Australasia | <i>p</i> | <<0.001                                          | <<0.001                           | <<0.001        | <<0.001                 | <<0.001       | <<0.001           |

are spinous (see Schmitt, 1940, figs. 18a, b). There are also possible differences in the form of the basal process of the uropods, in the color of live specimens, and in rostral shape (Moreira, 1905; Lemos de Castro, 1955). Because rostral shape is variable in *H. ensigera* and because there may be other statistical differences in variable features, most of the measurements upon *H. ensigera* were repeated upon the nine specimens of *H. braziliensis* in the USNM.

The ranges of values show complete overlap with *H. ensigera* data, but comparison of mean values gives data as shown below.

Number of segments of mandibular palp: 2.8889, cf. 2.7083 for nearest and largest *H. ensigera* value (Californian), difference highly significant ( $p \ll 0.001$ ).

Intermediate lobes of telson: On the criteria adopted above, the number of lobes is identical with *H. ensigera* from Chile, being unity throughout; however, most or all specimens of *H. braziliensis* possess small lobes just lateral to the intermediates, similar to those here



regarded as "vestigial" (see p. 6; also Schmitt, 1940, fig. 18b). These were only observed in three specimens of *H. ensigera*.

L/B rostrum: 1.1088, cf. 1.1021 for nearest *H. ensigera* value (Australasian), difference not significant ( $p$  0.8).

L carapace/L rostrum: 3.9650, cf. 4.0543 for nearest and lowest *H. ensigera* value (Californian), difference not significant ( $p$  0.4–0.3).

L/B cornea: 1.0556, cf. 1.2013 for nearest and lowest *H. ensigera* value (Australasian), difference just not significant ( $p$  0.2–0.1).

L eye/B cornea: 1.1544, cf. 1.3220 for nearest and lowest *H. ensigera* value (Australasian), difference highly significant ( $p \ll 0.001$ ).

Summarizing these differences, *H. braziliensis* differs from *H. ensigera* in having (1) in all cases, more spinous telson teeth and (probably) differently shaped basal processes of uropods; and (2) statistically significant differences as follows: a larger number of segments in the mandibular palp, a higher proportion of individuals with "vestigial" intermediate lobes of telson, a relatively broader cornea as indicated by lower L eye/B cornea ratios (and possibly by lower L/B cornea ratios).

### Discussion

There are three populations of *Hemisquilla* in the Pacific—one Australasian and two American. The latter are geographically separate (apart from a single juvenile from Panama).

Four possible morphological differences between the populations have been noted: number of segments in the mandibular palp, number of intermediate lobes on the telson, relative length of rostrum, and relative breadth of cornea. In each case there is considerable variability and overlap between populations.

An initial analysis showed that American and Australasian populations are morphologically distinguishable by statistical tests at a highly significant level. (These analyses also show hints of sexual dimorphism in some features and slight alterations of proportions with increasing specimen size.) At this stage one might conclude that the American and Australasian forms belong to two subspecies.

In further analyses a three-way comparison has been made, American material being treated under Chilean and Californian headings and compared with the Australasian. Of six features measured (two being different measurements of rostral proportions and two being eye proportions), the numbers of dissimilarities among the three populations are shown below.

|                             | highly<br>significant | just or<br>doubtfully<br>significant | not<br>significant |
|-----------------------------|-----------------------|--------------------------------------|--------------------|
| Australasian v. Californian | 6                     | 0                                    | 0                  |
| Chilean v. Australasian     | 3                     | 3                                    | 0                  |
| Chilean v. Californian      | 3                     | 1                                    | 2                  |



It is evident on the basis of present data that Chilean material is almost as distinct from the Californian as it is from the Australasian. The best schema to meet this situation is to regard each population as a subspecies. This conclusion is influenced by three factors:

(1) Only nine Chilean specimens were available for study. When additional material is measured, it seems likely that differences between Chilean and other material will become more significant.

(2) There is the possibility that detailed examination of colors of living specimens may afford further diagnostic criteria. Manning (pers. comm.) stresses the importance of color differences in other genera of stomatopods. In the present case it is possible that Chilean specimens may differ from Californian in having less yellow color on various appendages. Thus Nicolet's plate (1854, pl. 2, fig. 3) shows the following as green or bluish green: antennal scales, propodus of raptorial claws, and endopodites of uropods. They are canary yellow on living and recently preserved Californian specimens. To determine whether the differences are real or are artifacts, requires observations on fresh Chilean material.

(3) Distinctions between stomatopods at all levels are becoming increasingly fine, and subspecific distinctions must be finer still. This is emphasized by a comparison between *H. braziliensis* and the different groups of *H. ensigera*. Apart from two "firm" features the differences are of the same order as those between the different groups of *H. ensigera*. In these respects the Brazilian form shows no closer relationship to any one group of *H. ensigera* than to any other.

In view of the above, three subspecies of *H. ensigera* are therefore designated:

Chilean: *Hemisquilla ensigera ensigera*

Californian: *H. ensigera californiensis*, new subspecies

Australasian: *H. ensigera australiensis*, new subspecies

The distinguishing features, on the basis of present knowledge are as follows:

Mandibular palps: In *H.e. australiensis* 80% of the palps are two segmented and 20% three segmented. In *H.e. californiensis* the values are 25% and ca. 75%, respectively, and in *H.e. ensigera* they are 45% and 55%, respectively.

Intermediate lobes of telson: In *H.e. australiensis* about half the telsons have single lobes (45%) and about half (52%) two lobes. In *H.e. californiensis* over 95% have single lobes, and in *H.e. ensigera* all specimens examined have single lobes. On this basis *H.e. californiensis* and *H.e. ensigera* are indistinguishable.

Length/breadth ratio of rostrum: In *H.e. australiensis* the ratio is low (mean 1.10), in *H.e. californiensis* high (mean 1.34), and in *H.e.*

*ensigera* intermediate (mean 1.17). On this basis *H.e. australiensis* and *H.e. ensigera* are doubtfully distinguishable.

Length carapace/length rostrum ratio: In *H.e. australiensis* the ratio is high (mean 4.77), in *H.e. californiensis* low (mean 4.05), and in *H.e. ensigera* intermediate (mean 4.54).

Length/breadth ratio of cornea: In *H.e. australiensis* the ratio is low (mean 1.20), in *H.e. californiensis* high (mean 1.32), and in *H.e. ensigera* intermediate (mean 1.27).

Length of eye/breadth of cornea: In *H.e. australiensis* the ratio is low (mean 1.32), in *H.e. californiensis* intermediate (mean 1.46), and in *H.e. ensigera* high (mean 1.51). On this basis *H.e. californiensis* and *H.e. ensigera* are indistinguishable.

Type specimens of the three subspecies are designated as follows:

*H.e. australiensis*, male, carapace length, 28.5 mm, 12 miles E. Broken Bay, NSW, Australia, presented by H. Arnold, November 1946, AM reg. no. P.11695.

*H.e. californiensis* male, carapace length, 41.1 mm, Southern California, Anton Dohn coll., gift Venice Mar. Biol. Sta. 1909, USNM 50016.

*H.e. ensigera* Manning (pers. comm.) has informed me that the type of *H. ensigera* is a dry specimen in the collection of the British Museum (Natural History). I have not had an opportunity to study the specimen.

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